GROWTH ANALYSIS OF
SILURIAN ORTHOCONIC NAUTILOIDS

by R. A. HEWITT

ABSTRACT. Evidence from orthocone septal strength implies approximate depth limits of 200 m for the near-shore dwelling actinocerids, 500 m for large orthocerids, and no more than 1500 m for the small pelagic orthocerids found in 'graptolitic shales'. These estimates refer to the initial depositional depth of fully septate conchs; not the habitat depth of pelagic species, nor the occurrence of fragmented and reworked specimens. The further interpretation of the autecology of the large orthocerids must be based either on the distantly related, coiled genus *Nautilus*, or their large coleoid descendants. Studies of the growth rate of large orthocerids test their ecological similarity to large predatory coleoids. Cycles of lirae spacing in *Geisonocerina*, annulation amplitude in *Dawsonoceras*, and septal spacing in a variety of Silurian orthocones, show annual periodicities implying growth rates of about 100 mm per year. Large conchs with a length of 1·0 to 1·5 m had a protracted growth phase for over fifteen years, followed by at least one year as a slowly growing mature stage. The adolescent increase in body weight and mantle cavity volume is even less than that of *Nautilus*, suggesting little ecological similarity to coleoids.

ALTHOUGH the depth limits (Table 1) and swimming position of orthoconic nautiloids can be estimated from their shell morphology (Westermann 1973, 1977), it is difficult to interpret other aspects of their autecology. Perhaps the main dilemma results from their greater phylogenetic affinity with descendant lower Devonian to Recent coleoids (Bandel *et al.* 1983), than the primitive *Nautilus*. Although *Nautilus* resembles the coleoids in being a voracious predator (Saunders *et al.* 1978), it is not well equipped for rapid swimming by jet propulsion, diurnal or other rapid changes in depth, and visual capture of prey (Packard 1972, p. 292; Chamberlain 1981; Ward *et al.* 1981). Hewitt and Watkins (1980) pointed out that the small body size and mantle cavity volume of most pelagic orthocerids are inconsistent with interpretations involving intelligent and highly mobile, squid-like predators (McKerrow 1978; Gould 1983, p. 249). But the 0·5 to 3·0 m long orthocones found in relatively inshore Silurian facies are consistent with this autecological reconstruction.

This latter hypothesis was tested and rejected by an esoteric approach based on the view of Packard (1972) and Chamberlain (1981), that the volumetric increase in the mantle cavity during ontogeny was of paramount importance to cephalopods which capture prey, or avoid the cannibalistic attentions of their larger relatives, through efficient jet propulsion. Although *Nautilus* moves by jet propulsion, it has not developed the rapid escape reactions of coleoids and presumably obtains protection from an external shell and retiring habits. These and other ecological differences between Recent cephalopods are evident from their growth rates. One *Sepia* species probably grows a 0·5 m long shell and 10 kg body within two years (Packard 1972); but the tiny mesopelagic *Spirula* has a similar growth period. It grows about twenty chambers per year (deduced from Clarke 1970) compared to up to one per day in *Sepia* (Choe 1963). Cochran *et al.* (1981) and Ward *et al.* (1981) imply that *Nautilus* grows five to sixteen chambers per year, over a period of two to six years required to attain a body weight of about 0·5 kg. The growth rate and population turnover of the larger squids is sometimes even faster than that of *Sepia*, but there appears to be little reduction in growth rate due to shell formation (Packard 1972). Small cephalopod species, with inferior or redundant jet-propulsion adaptations, have a slow growth rate. If it can be shown that the large Silurian orthocerids had a growth rate which is equal to, or less than, that of *Nautilus*, it may be reasonably assumed that the ecological diversity of coleoids only developed after they lost the external shell of their ancestors.

TABLE 1. Strength indices of Carboniferous phragmocones calibrated by the penultimate chamber of *Nautilus* to estimate implosion depths. Terminology after Westermann (1977, 1982). The isotropic phosphate connecting rings in *Goniatites choctawensis* Shumard came from the same shale as brown sparry calcite connecting rings of *Bactrites quadrilineatus* Girty (Mapes 1979, sample M1). *Rayonnoceras* (M21–2 and M26) has a perispatium cemented with pyrite and isotropic phosphate, surrounded by inner sparry calcite and brown prismatic layers. These actinocerid rings were calculated as spherical membranes. The 'horny tubes' of Buckhorn Asphalt orthocerids are composed of bituminous aragonitic laminae. Despite these differences from the *Nautilus* 'horny tube', there is a correlation between connecting ring and septal strength indices. The proportion of nacre in the shell thickness δ_W is nac. %. The δ_W and septal spacing $\varDelta$ of coiled shells refers to the venter, and their r_i is half internal whorl height.

Genus * = from Westermann (1982)	Connecting ring				Septa					Shell wall		
	h μm	r μm	$\dfrac{100h}{r}$	Depth m	Depth m	δ_s μm	R mm	$\dfrac{1000\delta}{R}$	$\varDelta$ mm	δ_W μm	nac. %	r_i mm
Rayonnoceras	155	7300	2·1	260	200	133	22·7	5·9	17·5	1067	67?	20
Rayonnoceras	78	2700	2·9	360	264	68	8·7	7·8	4·7	530	64?	9
Nautilus	*74	*480	15·4	955	559	210	12·7	16·5	7·3	440	60	14
Nautilus	*150	*1160	12·9	800	800	778	33·0	23·6	26·0	910	75	48
Bactrites	78	456	17·1	1060	610	178	9·9	18·0	5·4	325	70?	7·65
'*Pseudorthoceras*'	27	157	17·1	1060	712	29	1·4	21·0	1·3	67	41	1·28
Goniatites	16	89	18·2	1129	—	7	—	—	0·8	34	—	0·38
Mitorthoceras	85	355	23·9	1482	1469	117	2·7	43·4	4·6	440	57	2·26
Goniatites	21	64	30·6	1900	—	6	—	—	—	54	—	0·22

The *Nautilus* chambers measured by Denton and Gilpin-Brown (1966) increased in volume at four times the exponential rate of the larger chambers of the 1·5 m long Ludfordian orthocerid measured by Hewitt and Hurst (1983). Since the latter taxon ('*Orthoceras*' *ludense* J. de C. Sowerby, resembling '*O.*' *alienum* Hall) increased the shell volume to balance the weight of both the body and posterior aragonite deposits, it is evident that either the body grew slower than in *Nautilus* or that over twenty to sixty-four chambers were added per year. But the evidence for a cycle of ten orthocerid chambers per year (Hewitt and Hurst 1983), supported here by additional studies, indicates that they were added at a similar rate to *Nautilus*. This conclusion that large Silurian orthocones had a slower increase in body weight than *Nautilus*, is related to the controversy over the use of ornamentation in growth-rate studies (Pannella 1972, 1975; Kahn and Pompea 1978; Pompea *et al*. 1979; Saunders and Ward 1979; Hewitt and Watkins 1980; Hughes 1981; Doguzhaeva 1982).

Orthocone morphology cannot be analysed purely as adaptative autecology, physiology, environmental cycles, or life history. It is, however, difficult to explain the major growth cycles of large orthocerids, except by seasonal growth-rate changes.

Since the annual growth cycles of *Sepia* are not sinuous it is preferable to analyse septal spacing and external lirae spacing by autocorrelation analysis. The method is discussed by Davis (1973, pp. 225–226) and the problems of analysis of nautiloid growth increments are reviewed by Hewitt and Hurst (1983). Briefly, the increment lag with the most significant parameter Z_L (which should be greater than 1·96) indicates the likely wavelength or repeat distance of a cycle. The parameter Z_L is only valid when the lag is less than one-quarter of the analysed series of growth increments and when there is no trend in the data. The latter can be standardized to remove ontogenetic trends, or larger growth cycles. Specimens are in Bristol Museum (BRSMG), Birmingham University (BU), Greene Memorial Museum (GMM), Milwaukee Public Museum (MPM), Field Museum (PE), Redpath Museum (RM), and McMaster University (S). Shell diameter was calculated from circumference.

CYCLIC VARIATIONS OF LIRAE SPACING

Kahn and Pompea (1978) admitted only three exceptions to their speculative thesis that orthocones grew eight to sixteen diurnal external transverse lirae (ridges) per synodic monthly chamber. Two were small aragonitic longicones from the Carboniferous Buckhorn Asphalt, i.e. *Mitorthoceras* (= '*Orthoceras unicamera* Smith') with forty-five lirae overlying each chamber and '*Pseudorthoceras knoxense* (McChesney)' with thirty lirae overlying each chamber. They proposed (p. 608) that these were unusual in being restricted to a 'shallow shelf and inland sea habitat (50–100 m depth)'. The criteria of Westermann (1973), cited by Kahn and Pompea (1978), shows that *Mitorthoceras* may have had the deepest-known nautiloid habitat (Table 1) and imply that only imploded or reworked nautiloids occur in strata deposited at depths much in excess of 1500 m.

A series of 315, 103 μm wide lirae, were studied in a 5 mm diameter *Mitorthoceras*. They averaged 44·8 per chamber in thin section. Asymmetric lirae of alternating amplitude grade into zones of narrow rounded lirae defined by striae. They originated as spherulitic prisms, radiating outwards from the nacreous layer of the shell wall. These 'cameral cycles' have thirty-four to seventy-nine increments (mean 55·4). Mural deposits formed over an interval of five to six cameral cycles (Crick 1982), and consist of 219 layers flanked by an outer translucent zone (180 μm) of seventeen layers, implying about one layer per lira. The siphuncle 'horny tube' has about twenty laminae per chamber. A retreat of the apertural mantle formed a high-amplitude lira passing into a translucent band within the outer prismatic layer. Five minor 'breaks' in growth were identified from the occurrence of these bands. They are associated with the narrow rounded lirae; but the retreat structure initiated the growth of asymmetric lirae. The number of lirae between breaks is: 87+, 4, 25, 8, 71, 4, and 115+.

The deep-water orthocerid displays gradational cycles of lirae spacing related to the internal layers of the conch, interrupted by mantle retreat events which may result from migration events. The latter should not be confused with unconformities defined by the pattern of the lirae, resulting from wounds or other local damage to the apertural mantle (Saunders *et al.* 1978, p. 138), and concentrated in mature growth stages.

Geisonocerina wortheni (Foerste) attained a diameter of 89 mm and a length of 1·48 m in the dolomites of the Telychian Brandon Bridge Member of Wisconsin (MPM 26360). A 558 mm series of 903 rounded lirae, defined by oblique external striae, was measured between diameters of 14 and 45 mm (MPM 25357 from Old Burlington Quarry, east side of White River). The lirae do not enlarge in proportion to the shell diameter, implying that fourteen were grown per chamber at the posterior end, compared to forty-five anteriorly. The anterior sutures and 180 mm long apex are missing. Unconformities occurring at an interval of 500 lirae increased lirae spacing. There are significant periodicities of eleven ($Z_L = 4·5$), nineteen ($Z_L = 4·3$), and ninety-four ($Z_L = 2·6$) lirae. The latter are related to eight major cycles of 110 ± 30 lirae defined by the variation in average lirae spacing within the shorter 'cameral cycles'.

An average of 6·32 festooned, 98 μm wide microlirae occur between the striae at the posterior end of this specimen, where there are bimodal cycles of twenty-one lirae ($Z_L = 2·5$) and a probable seasonal cycle of 128 lirae. If the poorly preserved microlirae are semi-diurnal they suggest that the periodicity of the lirae varied from 1·75 to 4·5 days.

Offshore Gorstian ?*G. recticinctum* (Blake) had a maximum diameter of 13 mm and a length of 150 mm. They show a similar ornamentation to *Mitorthoceras*. The external mould from Llangammarch Wells cited by Hewitt and Watkins (1980, p. 107) has cycles of lirae spacing with a lag of 18·0 ($Z_L = 3·87$ from 109 lirae). The 3 mm long cycles have a diameter of 2 to 4 mm. A series of eighty lirae (Watkins sample 214) show cycles of 31·17 lirae (lags 30 to 32 with $Z_L = 2·5$ to 2·6). The 7 mm long cycles have a diameter of 1·5–3·0 mm. They are too long to be 'cameral cycles' and give a plausible estimate of the number of solar days per synodic month.

CYCLES OF SEPTAL SPACING

Ludlow age longicones from Sardinia show minor cycles of septal spacing. *Sphaerorthoceras* (Serpagli and Gnoli 1977, pl. 4, figs. 2, 5, 6) contains six cycles between diameters of 0·7 and 4·0 mm. The mean wavelength/diameter ratio (4·7, range 3–9) differs from the mean periodicity of 9·27 chambers in showing no increase during ontogeny. *Arionoceras affine* (Meneghini) has a 30 mm long cycle of nine chambers at diameters of 5 to 10 mm (Serpagli and Gnoli 1977, pl. 6, fig. 4); but *A. submoniforme* (Meneghini) displays four cycles of four chambers (3–4 mm wavelength) between diameters of 1·3 and 3·4 mm (Serpagli and Gnoli 1977, pl. 7, fig. 2).

Typical cycles occur in the Waukesha and Racine Dolomites at Lannon, near Milwaukee. A 24 to 48 mm diameter *G. wauwatosense* (Whitfield) from the upper 0·04 m of the former horizon showed three cycles of eight chambers (mean length 91·2 mm and about ninety lirae). *Protokionoceras* from a 2 m 'Lannon Stone' section showed a 174 mm long cycle of nine chambers (diameter 21 to 25 mm); but more breviconic *Kionoceras* had six cycles of 4·1 chambers (32 to 51 mm diameter).

Kolebaba (1977, fig. 2) illustrated an asymmetric cycle of twenty-five chambers in a Gorstian *Vericeras ambigena* (Barrande) (diameter of 1·0 to 4·5 mm, length 21 mm). An '*O.*' *ludense* (Hewitt and Hurst 1983, fig. 4) has an asymmetric cycle of twenty-one, a major cycle of thirty-eight, and minor cycles of ten chambers. If the minor cycles are annual, they imply a growth period of ten to twelve years for 50 mm diameter longicones. This average growth rate is consistent with the growth period of ten years implied for 0·75 m long individuals of *G. wortheni* by lirae cycles. The 1·5 m long individuals of the two species were probably fully grown within twenty years and had a body weight of at least 1 kg.

SIGNIFICANCE OF ORNAMENTATION

Dawsonoceras has oblique annulations, ornamented with festooned transverse lirae forming 70 μm thick flanges. Lirae spacing is reduced over the thickened crests of the higher amplitude annulations. The annulation wavelength, which is also septal spacing, increased in proportion to the shell diameter until the diameter reached 30 mm, but then remained at 7–10 mm. Hughes (1981) found lirae composed of numerous lamellae. If the striae seen between lirae in annulation troughs define semi-diurnal increments, then these lirae formed in three solar or lunar days within a low-amplitude annulation with nine lirae, compared to 4·5 solar days in high-amplitude annulations with seven lirae. The implied monthly production of annulations was tested by assuming that the cycles of annulation amplitude had a seasonal origin.

The diameter of this 185 mm long increment increased from 38 to 50 mm. The twenty-one (BU Holcroft collection 56) annulations have an average of 7·1 lirae. The spacing of 158 lirae (up to fifteen measurements per lira at × 50) and the distance between the base of each lira and a ruler attached to the annulation crests, were used to calculate their diameter and cross-sectional volume (excluding flanges). The diameter lags of six ($Z_L = 8·7$) and twelve ($Z_L = 6·6$) lirae, corresponded to lags of six ($Z_L = 6·9$), twelve ($Z_L = 2·8$), and thirteen ($Z_L = 3·3$) lirae obtained by volume. Their weighted first harmonic was 6·14. Longer periodicities with Z_L over 1·96 have a weighted mean of 84·52 lirae; but the most significant lag is ninety lirae (Z_L of 4·4 by volume and 3·0 by diameter). A smoothed moving average showed volume growth maxima separated by a 116 mm length of 97·5 lirae and 13·21 annulations.

This seasonal cycle has four low amplitude annulations (35 mm length) with a mean of 9·25 lirae, compared to 6·67 lirae in the remaining high amplitude annulations resulting from optimum growth. Similar cycles were seen in eight *Dawsonoceras* (Table 2). Racine Dolomite specimens show sixteen other cycles of annulation amplitude, with a mean of 9·50 annulations. Of these only the Dudley specimen (56) encrusted by *Halysites* and the Sussex specimen from a fissure in a bioherm without corals, grew one annulation per month. Adding together long specimens from these and other localities, we arrive at an estimate of 132 annulations between diameters of 3·8 and 57·3 mm. Conch

length increased at a single linear growth rate over the last ninety-three annulations, representing 780 mm out of a total length of 975 mm (another has forty-nine expanding annulations in 427 mm).

The existence of cyclic variations in ornamentation restricts the scope of functional interpretations of structural elements, camouflage patterns, and devices for reducing drag by increased surface roughness (Chamberlain 1981, p. 299). A depth limit of 500 m, implied by the septal strength index of Indiana *Dawsonoceras* (Laurel Member, Flower 1962; δ_s/R . $1000 = 15$) appears excessive for life over epicontinental carbonate facies. *Dawsonoceras* from the argillaceous Rochester and middle Elton formations display unusually low annulations and narrow lirae. Thus if there was any advantage in the development of annulations, it was likely to be related to the greater value of camouflage over limestone facies than in dark, turbid environments.

The apertural end of a large specimen from argillaceous dolomite (RM 2644) shows a well-defined zone of 109 narrow lirae without annulations. This observation and the general tendency of mature nautiloids to show a greatly reduced septal spacing, suggests that the low amplitude phases of the growth cycles represent a less extreme reduction of growth rate than that associated with maturity. In contrast, the vast majority of coleoids grow rapidly, breed once, and then die (Packard 1972). The 1 m long *Dawsonoceras* grew at a slow and periodically variable rate for about fifteen years, grew even more slowly when mature, and may have lived longer without increasing body weight. The growth and breeding characteristics of coleoids are not a primitive trait.

It is not clear whether the cycles resulted from seasonal migrations between two different environments; or local changes in temperature, hydrography, and food supply through the year. The paucity of abrupt changes in growth and apertural unconformities supports the latter view. A sedentary life as bentho-necton would explain variation in growth cycles and ornamentation between localities (Table 2) and the problematical stratigraphic value of *Dawsonoceras* 'species' defined by gradational variations in these characters. Flower (1942, 1962) reviews some of these difficulties.

This interpretation is consistent with the evidence from lirae spacing and septal spacing in less-ornate orthocerids. Together they imply a mode of life combining the buoyancy of *Nautilus* and the

TABLE 2. *Dawsonoceras* show variation in their lirae/annulation ratio (*L/a* on left) which is not a function of mean diameter (dia.) or diameter/annulation wavelength (dia./*A*). Cycles defined by *L/a* were one to four times longer than their diameter (Yr/dia.). Specimens are from: Homerian limestones of Dudley (BU Holcroft Collection 33, 56, 76; Ketley Collection 476); Sheinwoodian shales of Rochester Formation at Lockport (RM '1138'); Sheinwoodian Waukesha Dolomite of Lannon (PE 18943, 19017) and Sussex; Racine Dolomite of Milwaukee (including GMM 12965, 12445, and a 26th Street Quarry specimen); Homerian Lockport Dolomite, all members in Hamilton area (BRSMG Cc829; RM 2644, 2648; S699). n = number of annulations in sample.

Sample	Annulation sample						Seasonal cycles					
	n	dia. mm	range mm	dia./A	*L/a*	range	Sample	dia. mm	Yr/dia.	Cycle		
										L	a	L/a
Dudley	57	40	22–57	4·8	8·17	5–18	BU 56	47·5	2·4	97	13	7·4
							BU 476	26·5	2·5	81	9	9·0
Rochester	24	31	26–36	6·2	8·83	5–12	RM 1138	28·0	1·9	84	10	8·5
							RM 1138	31·5	1·1	65	7	9·3
Waukesha	43	29	21–38	3·5	9·21	4–16	Sussex	26	3·8	84	13	6·5
							Sussex	34	2·2	103	11	9·4
Racine	22	34	12–51	3·6	11·84	7–10	12965	31·0	2·3		8	7·0
							12445	41·5	2·2		10	10·5
							26th st.	48·8	1·4		7	11·0
Hamilton	48	39	19–45	4·4	13·00	9–23	RM 2648	40·6	2·2	112	9	12·4
							RM 2644	44·6	1·5	74	5	14·8

swimming position of coleoids with the ponderous feeding behaviour of some carnivorous gastropods and arthropods. In addition, there were small orthocerid species, which probably drifted with the zooplankton rather than migrate like large squids.

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Note added in press. Although Landman (1984) has rightly questioned the assumptions of Doguzhaeva (1982), it would be unwise to base interpretations only on our present knowledge of *Nautilus*. A recent volte-face by Ward appears to have increased the chance that fossil nautiloids formed one or two growth increments per solar day, as a result of vertical migrations avoiding sunlight (Ward *et al.* 1984). The well documented migrations across the reef front in Palau and the lateral peregrination of one individual, recorded as 16 km in ten days, indicates that *Nautilus* is an active member of the bentho-necton. Moreover, the life-span of seventeen to twenty years deduced by a questionable extension of growth rates seen in sub-mature *Nautilus* (Saunders 1984), is inconsistent with the evidence suggesting that a juvenile, barnacle encrusted *Nautilus* formed over sixteen chambers in 340 days (Landman 1983). But these debates do not seriously alter the above conclusions about Silurian nautiloids.